PHYTOGEOGRAPHIC RELATIONSHIPS OF PTERIDOPHYTES BETWEEN TEMPERATE NORTH AMERICA AND JAPAN[1]

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The pteridophyte flora of North America comprises 325 species (Tryon, 1969) and the non-endemic species among them are referred to four geographic groups: circumpolar, amphioceanic, tropical, and Mexican. Japanese pteridophytes include about twice as many species as the North American, although the Japanese Archipelago is much smaller. The Japanese species are also more complex taxonomically and phytogeographically (Tagawa, 1959; Ohwi, 1965). The distribution pattern of the Japanese ferns is considered to be related to climatic zones by some authors including Nishida (Graham, 1972). They can be arranged roughly in the following phytogeographic groups: circumpolar, Eurasian, trans-Pacific (related to North America), Sino-Himalayan, and tropical Southeast Asian. The phytogeographic relationships between North America and Japan are found primarily in the temperate to boreal species.

Since Asa Gray's time, phytogeographic relationships between eastern North America and eastern Asia have been discussed by many authors for pteridophytes as well as for flowering and non-vascular plants (Hultén, 1958, 1962; Li, 1952; Graham, 1972; Tryon, 1969; Tryon & Tryon, 1973). In spite of the accumulation of data, there still is no complete phytogeographic analysis of the biological relationship between eastern North America and the Far East. The complex geohistory often is taken into account and the floristic comparison often is made rather theoretically. Changes in land and climate in the Northern Hemisphere that have occurred since the Tertiary have given rise to replacement of boreal, temperate, or warm floras in the areas concerned, and have enabled plants to migrate between the North American and Asian continents via the Bering Strait (chiefly dry land in the Tertiary) and Aleutian chain. This migration probably occurred several times and in either eastward or westward directions. Similar events would have occurred in a south to north direction between temperate and tropical regions. Specia-

tion and gene-flow caused by the geographic isolation and reunion might have taken place in both those areas. The fern floras of North America and eastern Asia include identical or related species. Some of the identical species might be younger and widespread in the Northern Hemisphere, whereas some related species might be older and become restricted to either North America or eastern Asia.

Phytogeographic relationships of fern floras result from species migration that is initiated primarily by spore dispersal. Spore viability varies from about a week to more than several years; green spores are especially short-lived compared with non-green spores. It is reported that fern spores resist, to a considerable extent, physical and chemical environmental stress from low temperature, desiccation, UV- and X-rays, and other factors that operate during the transport (Page, 1979). Tryon (1970) argued the effectiveness of long dispersal of fern spores in island fern floras and estimated that "distances up to 300 miles are only a slight barrier to the migration of a fern flora and that a distance of 500 miles is not a significant barrier." In spite of this, most fern species are restricted in distribution and only a limited number have wide ranges. This means that the dispersal or migration of most ferns is regulated by some unknown factors. Page (1979) pointed out that many biotic and non-biotic ecological relations are involved in migration. In his study on genetic features of disjunct fern populations, Klekowski (1972) considered that the long-distance establishment and future evolutionary processes of fern populations are dependent on the mating system (intragametophytic vs. intergametophytic fertilization) and genetic variability as well as geographic reproductive isolation. Our knowledge of the mechanism of spore dispersal and species establishment at a new locality is still insufficient to fully understand the phytogeographic relationships of the fern flora in question, for which further experimental and field studies are desired.

In this paper the phytogeographic relationships between temperate North America and eastern Asia are examined, based on the presumed taxonomic affinities of the pteridophyte species concerned. In analyzing the similarity between the two areas, it is intended to elucidate 1) the similarity or difference between the two areas, especially in the composition of their floras, and 2) the taxonomic relationship between the apparently identical or vicarious species known in the two areas.

FIGURE 1. The number of common species among Hokkaido, northeastern North America, and Europe. For explanation see the text.

FLORISTIC SIMILARITY

Of 116 species occurring in eastern North America (Morton, 1968) 52 species (45 percent) are also native to Japan, and the figure approaches that for the bryophytes that have the similar dispersal means of airborne spores. Of the 52 common species, 45 species (39 percent) are either widespread in the temperate to boreal Northern Hemisphere or are cosmopolitan, and seven species (cited below) are restricted to eastern Asia, including Japan. The species common to these two areas have their center of distribution in Japan in central and northern Honshu and Hokkaido, whereas southwestern Japan is inhabited by many Sino-Himalayan and Malesian elements. For convenience, Hokkaido will be used for comparisons (Fig. 1). Hokkaido, the northernmost island in Japan of not more than 80,000 km², has a temperate to sub-boreal flora. This flora includes 122 pteridophyte species, a number that is almost equivalent to the 116 species in temperate eastern North America. Forty species (33 percent) of the Hokkaido pteridophyte flora have a circumboreal or cosmopolitan distribution (of a possible 45), seven species are of temperate North America–eastern Asian distribution, and 75 species are of other distribution patterns. Including the 40 widespread species, 43 (35 percent) of Hokkaido pteridophyte species are common to those of Europe where 141 species occur (Tutin et al., 1964). Fifty-five species (46 percent) of eastern North American species are distributed also in Europe. Northwestern North America has a pteridophyte flora consisting of 81 species (Hitchcock & Cronquist, 1955), of which 37 (46 percent) also occur in Japan. Of these, 34 species are circumboreal and three are among the seven species of the eastern North America–eastern Asian distribution pattern.

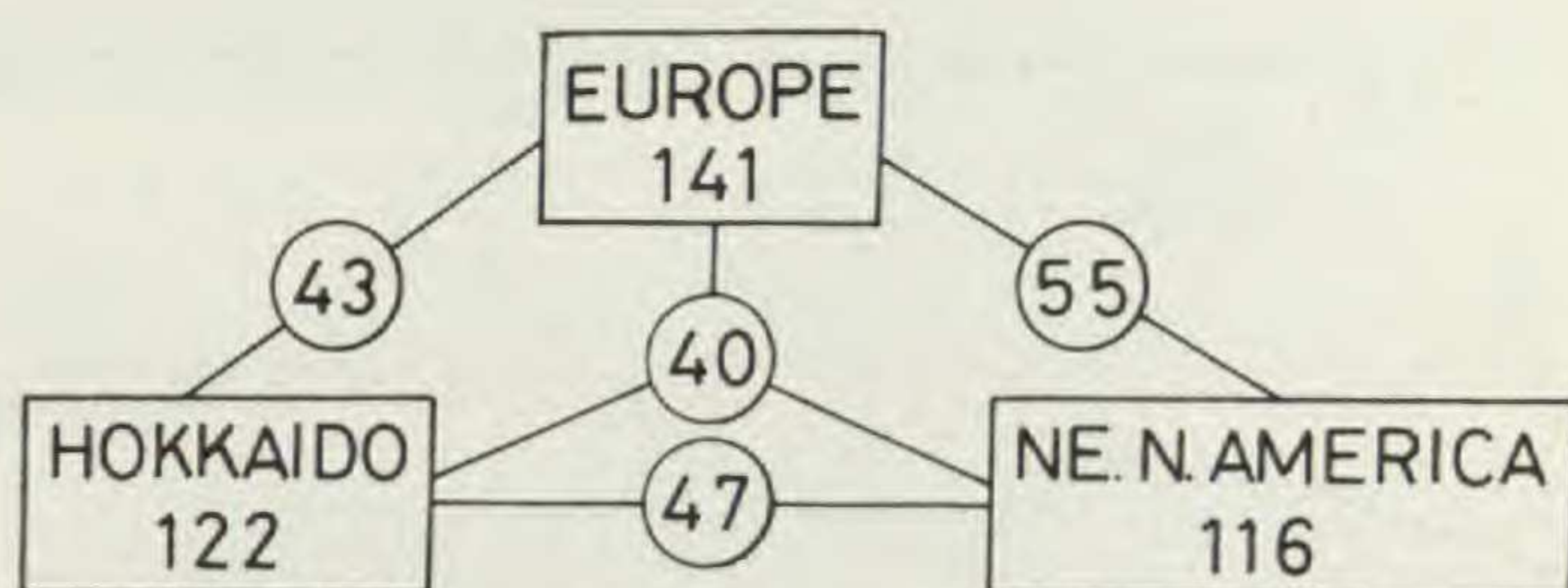Li (1952) stated that the distribution patterns of the pteridophytes are different from those of the seed plants that have different means of reproduction and dispersal, and that whereas the floristic relationship of the seed plants between temperate eastern North America and eastern Asia is primarily generic, few fern genera, if any, indicate such a relationship. By contrast, Tryon and Tryon (1973) compared the fern species in both areas and pointed out that the phytogeographic relationship of pteridophytes in both areas is strong and that about 20 percent of the species in eastern North America show disjunct affinities with identical or related species in eastern Asia.

The above floristic comparison shows that most of the apparently identical species (some of which vary infraspecifically) known in temperate North America and Japan are circumboreal and occupy one-third to two-fifths of the pteridophyte flora in every area of eastern North America, Hokkaido, and Europe. The other several species are restricted to both areas in question. The relationships clearly imply a former, more widespread, similar temperate fern flora that was broken by climatic change in the late Tertiary (post-Miocene).

IDENTICAL AND VICARIOUS SPECIES

The phytogeographic relationship between temperate North America and eastern Asia is strongly suggested by the apparently identical or vicarious species that are confined to the two areas. The seven apparently identical species are: *Lycopodium obscurum, L. sitchense, Osmunda cinnamomea* (eastern; extending into tropical America as var. *imbricata*), *O. claytoniana* (eastern), *Adiantum pedatum, Onoclea sensibilis* (eastern), and *Polypodium virginianum* (eastern). A few eastern Asiatic pteridophytes extend to the northwestern part of North America, Alaska, and Pacific Canada: *Lycopodium chinense, Selaginella sibirica,* and *Mecodium wrightii.*

Tryon and Tryon (1973) cited examples of several vicarious species between North America
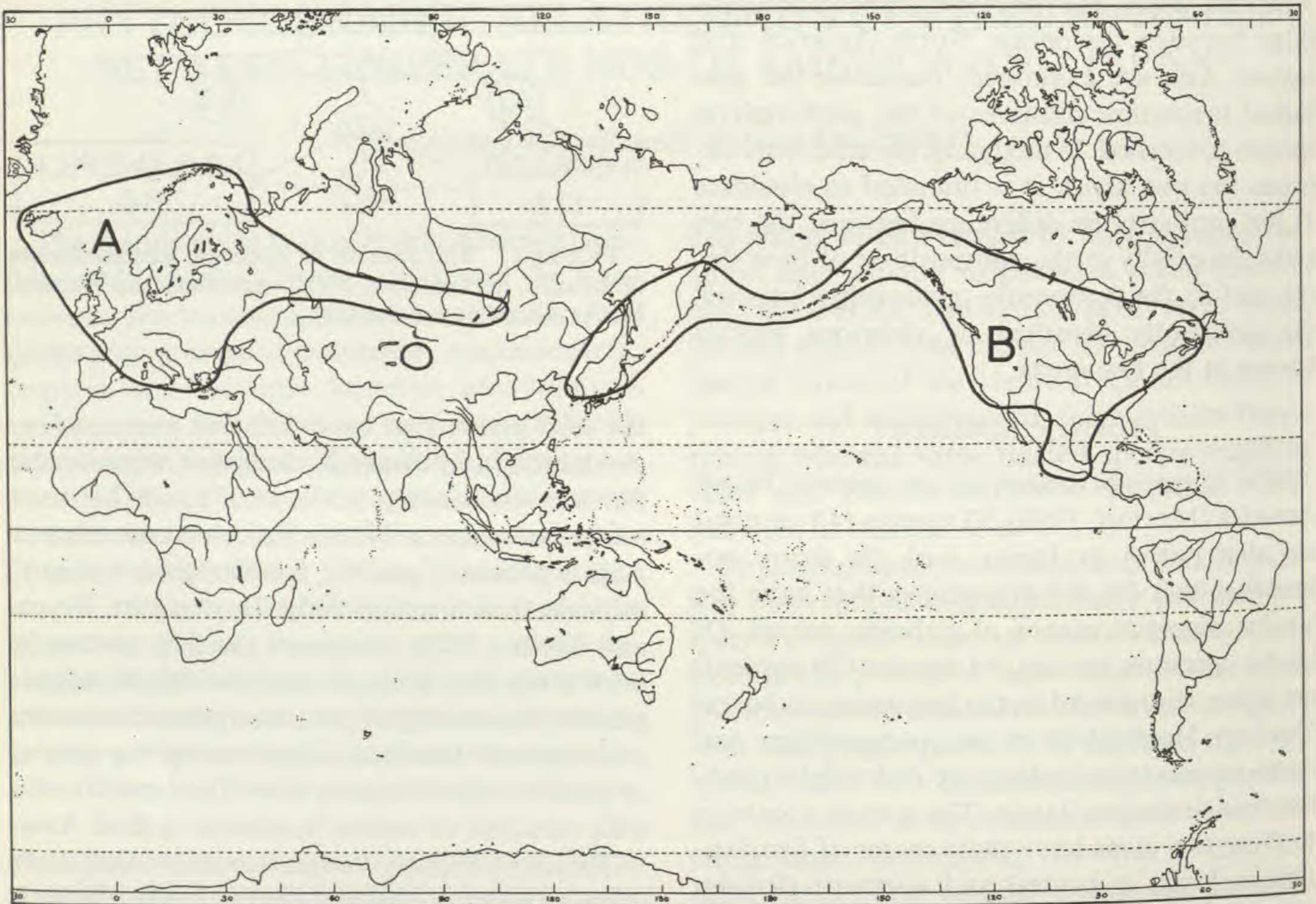
FIGURE 2.   Distribution of *Equisetum hyemale*.—A. var. *hyemale*;—B. var. *affine*. (After Hauke, 1963.)

and eastern Asia: *Dennstaedtia punctilobula* of eastern North America vs. *D. appendiculata* and *D. scabra* of eastern Asia; *Thelypteris noveboracensis* of eastern North America and *T. nevadensis* of western America vs. *T. beddomei* and *T. nipponica* of eastern Asia; and *T. simulata* of eastern North America vs. *T. glanduligera* and *T. japonica* of eastern Asia. *Asplenium rhizophyllum* of eastern North America and *A. ruprechtii* of eastern Asia are a well-known example of a vicarious species pair. They are often treated as comprising a separate genus *Camptosorus* because they are typologically different, especially in their reticulate venation, from the other species of *Asplenium*. The following is a discussion of some identical or vicarious species of phytogeographic interest.

Equisetum hyemale.   Of the ten species and several hybrids of *Equisetum* that occur in temperate North America, eight are also native to Japan (Hauke, 1963, 1978): *E. sylvaticum, E. pratense, E. arvense, E. fluviatile,* and *E. palustre* of the subgenus *Equisetum* and *E. hyemale, E.*

variegatum, and *E. scirpoides* of the subgenus *Hippochaete. Equisetum hyemale* has two varieties, vars. *hyemale* and *affine,* of which the latter shows the North America–eastern Asian relationship. *Equisetum hyemale* var. *affine* is distributed in North America and eastern Asia, whereas var. *hyemale* occurs in Eurasia, extending eastward to Asiatic Russia and westernmost China (Fig. 2). The former variety is considered to have expanded its distribution range in a westward direction (Hauke, 1963).

Hauke (1963) speculated on the phytogeographic evolution of subgenus *Hippochaete,* based on a phylogeny inferred from morphology. It originated in South America and radiated northerly; several species were differentiated in the process. The most primitive member of the subgenus is *E. giganteum,* distributed in South America. An *E. giganteum*-like ancestor likely gave rise to *E. ramosissimum* with two subspecies, the Eurasian ssp. *ramosissimum,* ranging from Europe, Mediterranean Africa, and South and East Africa to Japan, and ssp. *debile* ranging
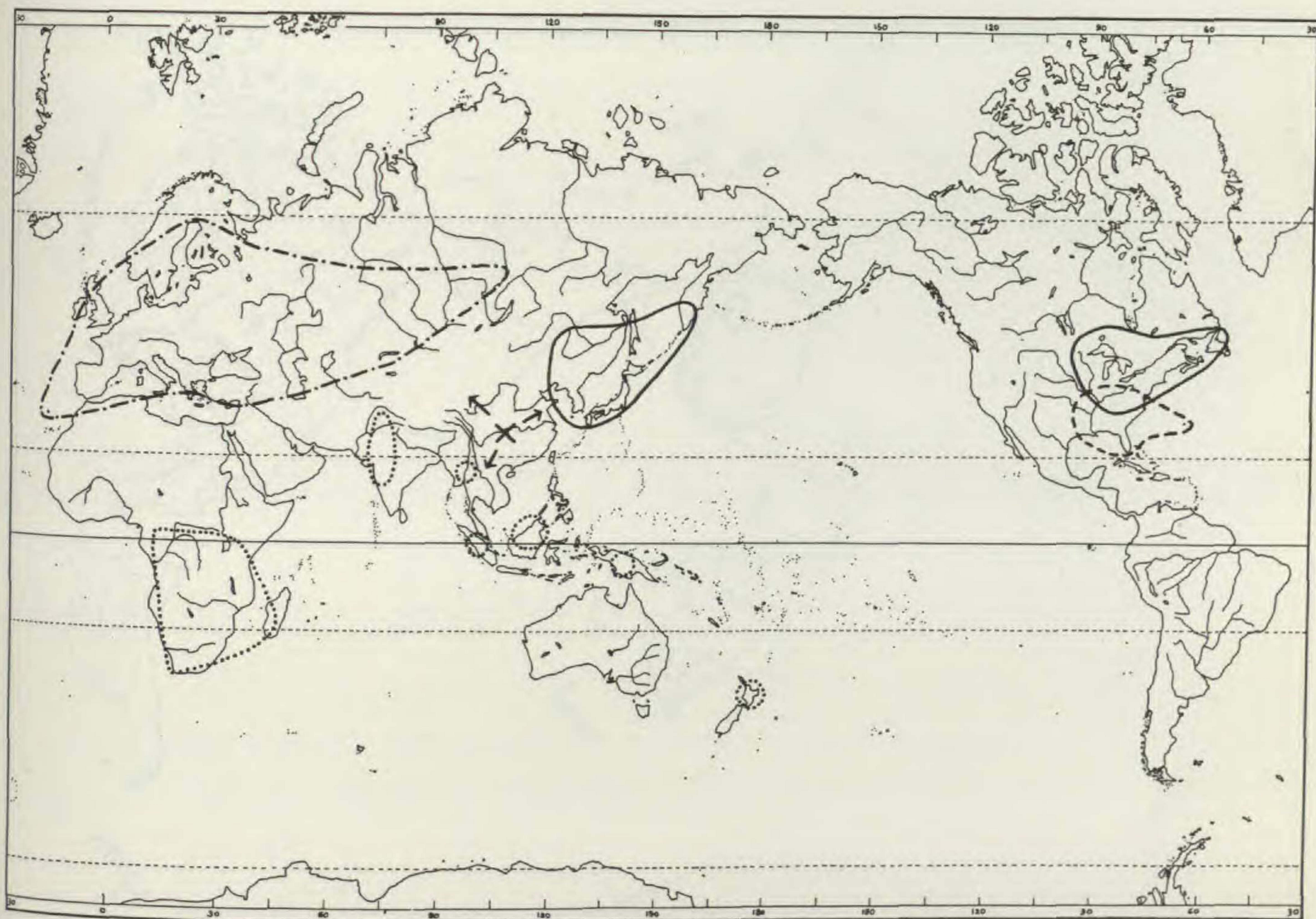
FIGURE 3. Distribution of *Thelypteris palustris*. Solid line, var. *pubescens*; dashed line, var. *haleana*; dotted line, var. *squamigera*; dash and dot, var. *palustris*. (After Tryon, 1971.)

from India to Fiji through Southeast Asia. From the *E. ramosissimum* complex originated two American species, *E. myriochaetum* of Central and South America, and *E. laevigatum* of western North America. "*Equisetum hyemale* developed in southwestern North America, presumably from a common ancestor with the *ramosissimum*-complex, and spread throughout North America. It crossed the North Atlantic land bridge . . . and migrated throughout Europe and across Siberia, there occurring as var. *hyemale*" (Hauke, 1963), whereas var. *affine* crossed the Aleutian chain to eastern Asia.

Thelypteris palustris. This species is worldwide in distribution except in South America (Fig. 3) and is diversified in several characters. It consists of the following four varieties: var. *pubescens* of northeastern North America and eastern Asia; var. *haleana* of the southeastern United States and Bermuda; var. *palustris* of Eurasia; and var. *squamigera* of Africa, India, Burma, Thailand, Sumatra, Borneo, New Guinea,

and New Zealand. The classification of this diverse species varies according to the author. Tryon (1971) followed Fernald (1929) in comparing the spore characters of four varieties of *T. palustris*. She suggested that continental southeastern Asia is the center of radiation of this species. It might in turn be suggested that the distribution range of var. *pubescens* has been established by eastward migration from Asia to North America.

Thelypteris noveboracensis and T. nipponica. These two species are often referred to as representing a typical example of vicariants with disjunct distribution (Tryon & Tryon, 1973). *Thelypteris noveboracensis* occurs in eastern North America and *T. nipponica* is distributed in Saghalien, the Kuriles, Hokkaido, northern and central Honshu, Korea, and central and western China. They belong to *Parathelypteris* sensu Holttum and are similar to each other in phenetic features with the exception of the scale features and soral position. The chromosome
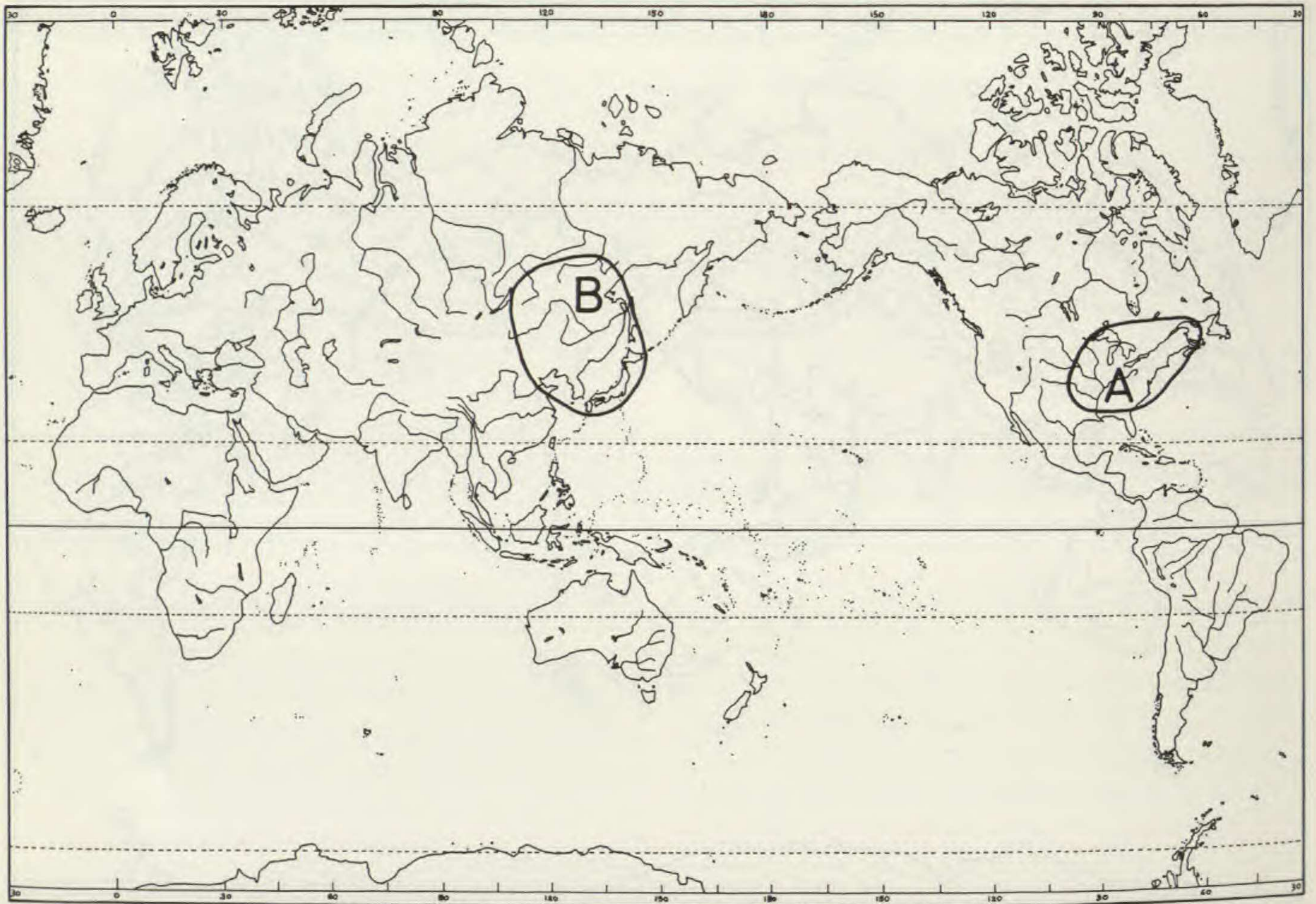
FIGURE 4. Distribution of *Asplenium rhizophyllum* (A) and *A. ruprechtii* (B).

number of *T. noveboracensis* is reported as *n* = 27 (Tryon & Tryon, 1973) and that of *T. nipponicum* as *n* = 62 (Hirabayashi, 1970). The latter is often considered to be related to the Asian *T. beddomei*, the chromosome number of which is *n* = 31, and *T. beddomei* is a suggested vicariant of *T. nevadensis* of western North America. In spite of their phenetic resemblance, it is necessary to revise them, and so we refrain here from discussing the geographic relationship between *T. noveboracensis* and *T. nipponica*. The eastern North American *T. simulata* is also comparable with the Asiatic *T. glanduligera*, although we have no conclusive remarks on the phytogeographic relationship between the two species.

Asplenium rhizophyllum and A. ruprechtii. *Asplenium rhizophyllum* is known in restricted areas of eastern North America from Quebec to Minnesota, Georgia, Alabama, Kansas, Oklahoma, and Michigan, and *A. ruprechtii* is found in eastern Asia in eastern Siberia, northern and north-eastern China, Korea, and Japan (Fig. 4). These species are isolated from the other species of *Asplenium*, especially in their special habit of gemmiferous tips of the simple fronds (often called walking) and anastomosing sagenioid venation; the two species are discriminated by the form of the leaf base. Both often grow on limestone, although they can grow also on non-calcareous rocks. It is certain that these two are closely related, although we have no fossil evidence documenting the migration and speciation of these taxa.

Deparia acrostichoides. The only North American representative of the genus *Deparia* is distributed in the temperate eastern region (Fig. 5). It is closely related to eastern Asiatic vicariants, *D. pycnosora* and allied species of section *Lunathyrium*, differing principally from the latter in possession of creeping rhizomes with more widely spaced leaves. Section *Lunathyrium* has its center of distribution in eastern Asia with many diverse species and therefore it probably
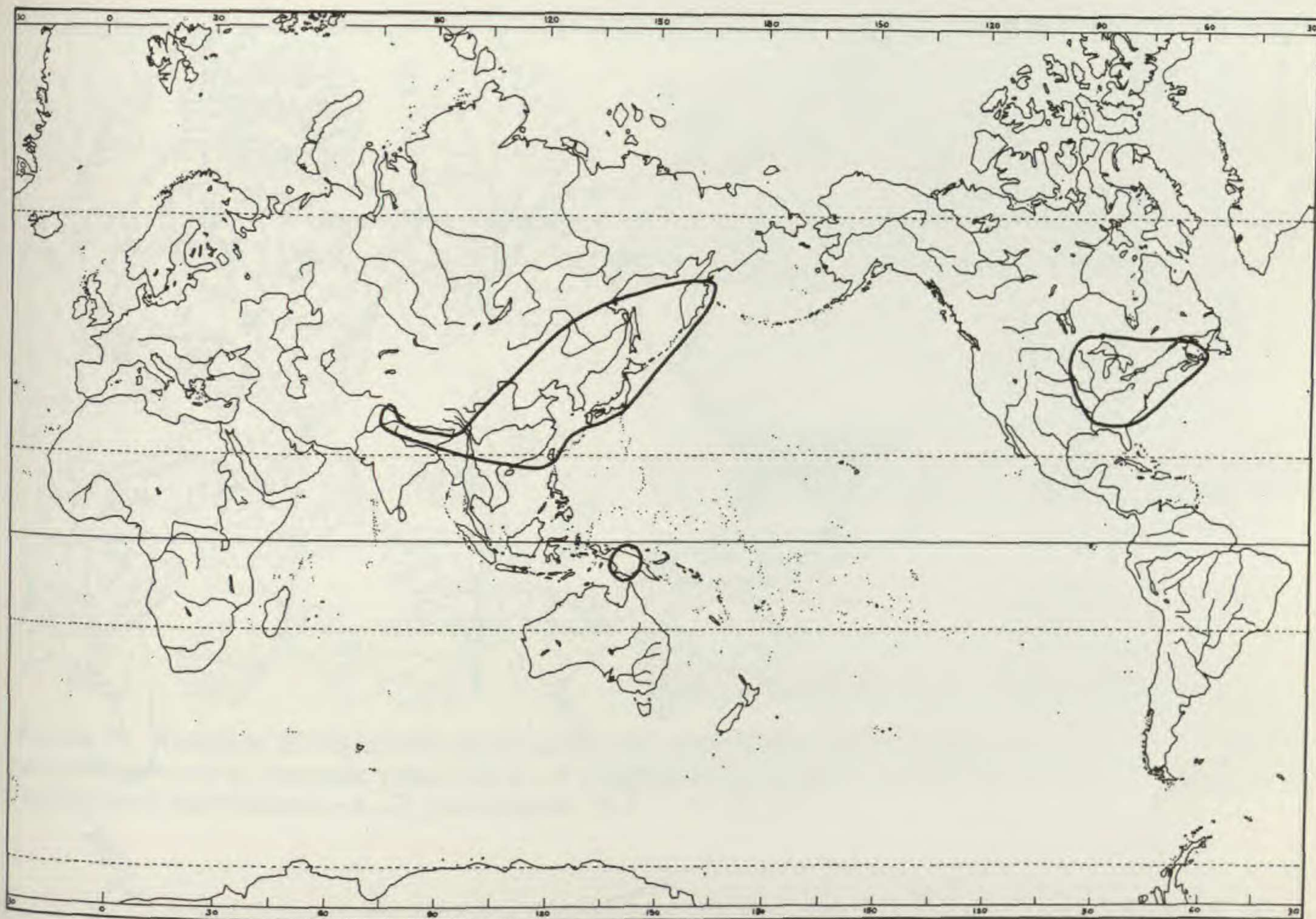
FIGURE 5.   Distribution of *Deparia* section *Lunathyrium*. See text for discussion.

originated there. It seems likely that a part of the *D. pycnosora* group migrated in an eastward direction and gave rise to *D. acrostichoides*.

Diplazium pycnocarpon. This species is the only member of *Diplazium* from temperate eastern North America (Fig. 6), although it is still commonly placed in *Athyrium.* It possesses several specialized aspects, including a temperate distribution (in contrast to a tropical and subtropical distribution of the majority of *Diplazium*), and frond morphology (particularly in the veins, which reach the concave pinna margin). *Diplazium pycnocarpon* seems to be, as stated by Tryon and Tryon (1973), a vicarious species of a *D. javanicum* group from east and southeast Asia (Fig. 6), which has usually been segregated as a distinct genus, *Diplaziopsis*, by the imparipinnate fronds, anastomosing veins, and vaulted sausage-shaped sori (Fig. 7). This Asiatic group is in turn closely related to a *D. heterophlebium* group, which has similar anastomosing venation and pinnate fronds without distinct terminal pin-

nae (Fig. 7), and thereby has been separated as *Dictyodroma* by some taxonomists. Kato (1977) supposed that the *D. javanicum* group and the *D. heterophlebium* group are related to tropical American *D. marginatum* (most often known as *Hemidictyum marginatum*) with a more elaborate reticulate venation (Fig. 7). These species are distinct not only morphologically but also cytologically. It is reported that the basic chromosome number of the *D. javanicum* group and the *D. heterophlebium* group is $x = 41$, a common number of the genus *Diplazium*, whereas *D. pycnocarpon* has $x = 40$ and *D. marginatum* $x = 31$ (Love et al., 1977).

It is possible that *D. pycnocarpon* is derived from a *D. marginatum*-like ancestor, but more likely it was established as a specialized temperate species with a closer affinity to the Asiatic species.

Gymnocarpium dryopteris. The genus *Gymnocarpium* comprises six species that are classified into two subgenera, *Gymnocarpium* of five
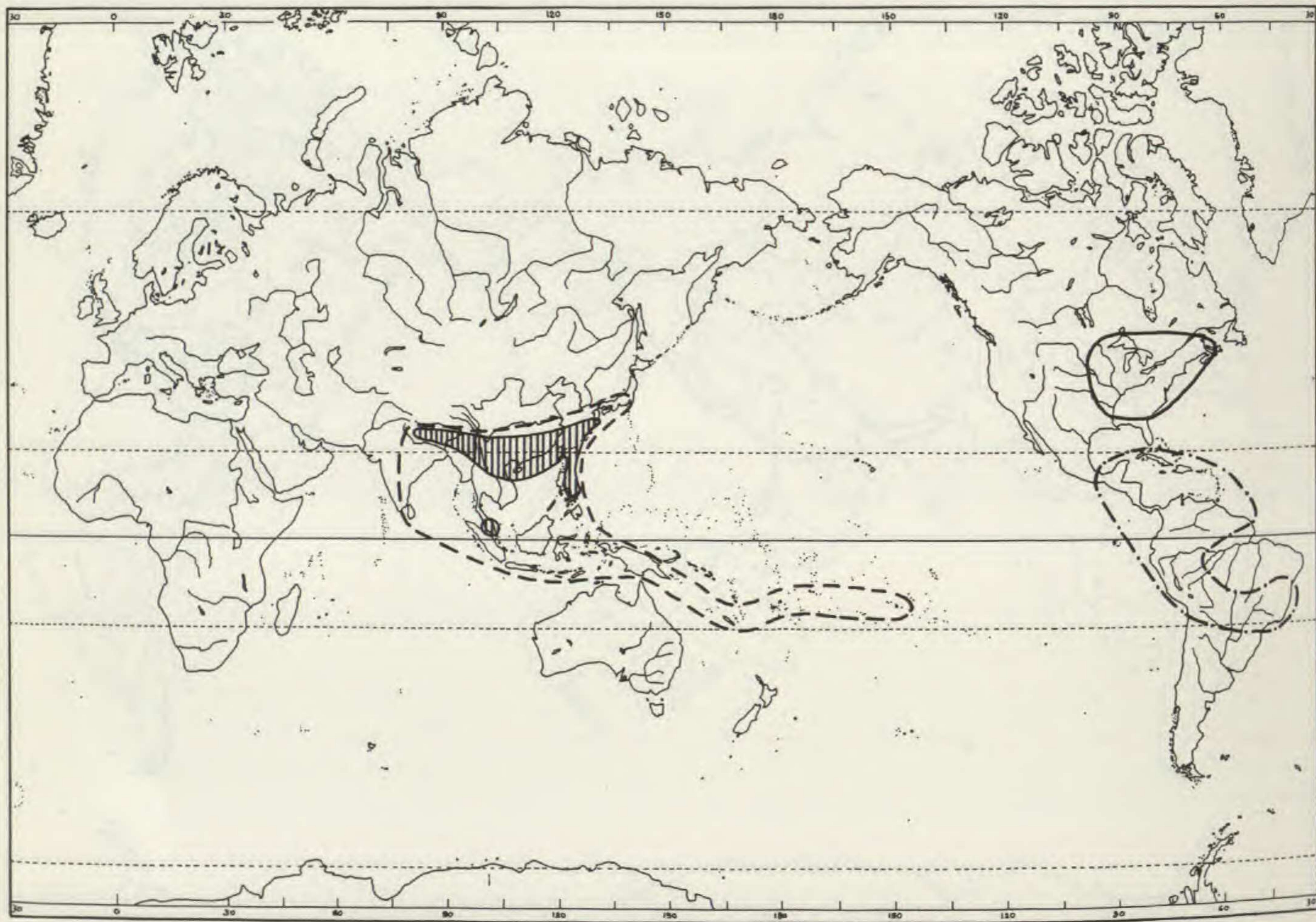
FIGURE 6.   Distribution of *Diplazium pycnocarpon* and presumably related species. Solid line, *D. pycnocarpon*; dashed line, *D. javanicum* group (*Diplaziopsis*); vertical lines, *D. heterophlebium* group (*Dictyodroma*); dash and dot, *D. marginatum* (*Hemidictyum*).

closely related species, and *Currania* with one species, *G. oyamense*. Three of the species are restricted to Asia: *G. remote-pinnatum* in Taiwan, *G. fedtschenkoanum* in Tadzhikistan, and *G. oyamense* in Nepal, continental China, Taiwan, Japan, Luzon, and New Guinea, whereas the other three are widely distributed in Asia, America, and Europe (Sarvela, 1978). From its taxonomic relationships and geographic distribution it can be suggested that the genus originated and diversified into two subgenera in Asia and spread to Europe and North America. Cytological studies show that *G. dryopteris* ssp. *dryopteris* has $2n = 160$ and ssp. *disjunctum* $2n = 80$, *G. jessoense* ssp. *jessoense* $2n = 80$, *G. robertianum* $2n = 160$, and *G. oyamense* $2n = 80$ and 160, suggesting that the diversification of the genus arose mostly at the diploid level. The tetraploid *G. dryopteris* ssp. *dryopteris* has a circumboreal distribution and the diploid ssp. *dis-*

junctum has a more restricted range in Saghalien, southern Kamtchatka, and northwestern North America (Fig. 8). It is suggested that the wide distribution of the species is the result of a recent expansion of a polyploid taxon.

Onoclea sensibilis. The onocleoid ferns are composed of two genera, *Onoclea* and *Matteuccia*, and five species that include a species of putative hybrid origin (Kato & Sahashi, 1980). *Onoclea* consists of two species, *O. sensibilis* and *O. orientalis*. The former is separated into two varieties, var. *sensibilis* of eastern North America and England (probably introduced), and var. *interrupta* of eastern Asia, which differs from var. *sensibilis* in possessing more widely-spaced fertile pinnules (Fig. 9). Paleobotanical evidence shows that in the Cretaceous and Tertiary the *Onoclea sensibilis* group was diversified and distributed more widely than the present, and was known from Alaska, Canada, the United States,
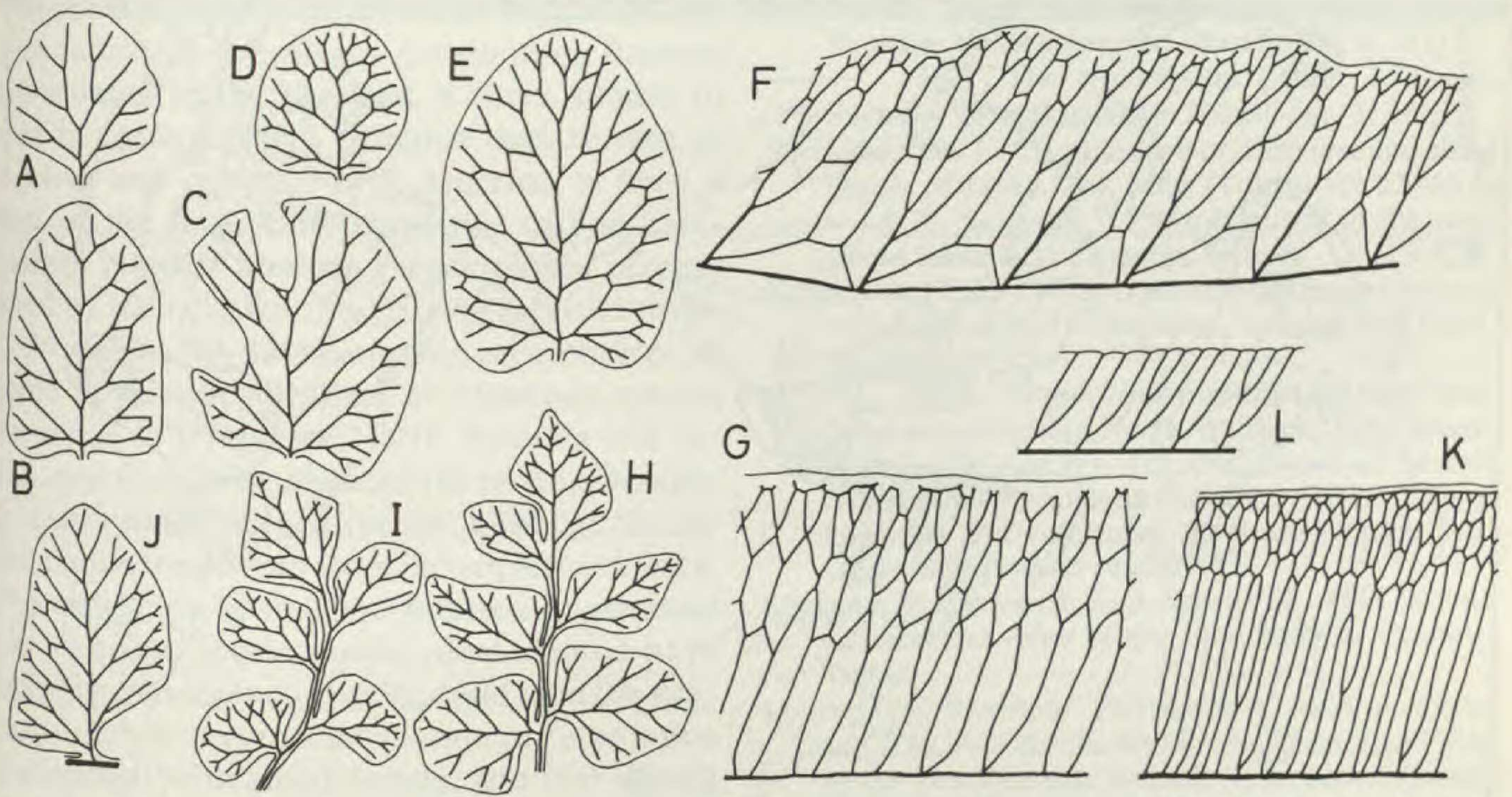
FIGURE 7.   Venation of *Diplazium pycnocarpon* and presumably related species.—A–F. *D.* (*Dictyodroma*) *heterophlebium*:—A–E. Juvenile plant.—G–J. *D.* (*Diplaziopsis*) *cavalerianum*:—H–J. Juvenile plants.—K. *D.* (*Hemidictyum*) *marginatum.*—L. *D. pycnocarpon.* A–J, L ×1, K ×½.
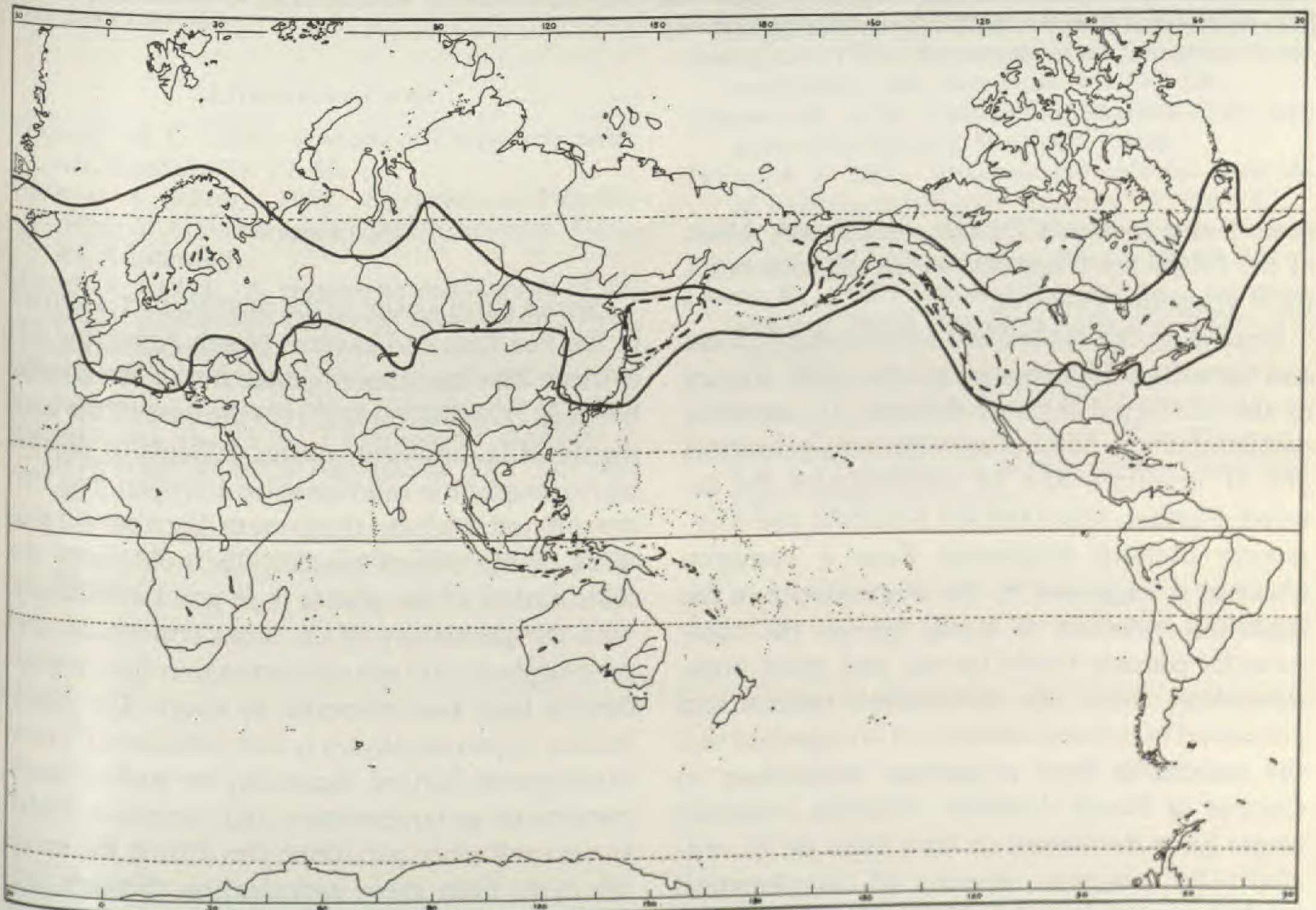

FIGURE 8.   Distribution of *Gymnocarpium dryopteris.* Solid line, ssp. *dryopteris*; dashed line, ssp. *disjunctum.*
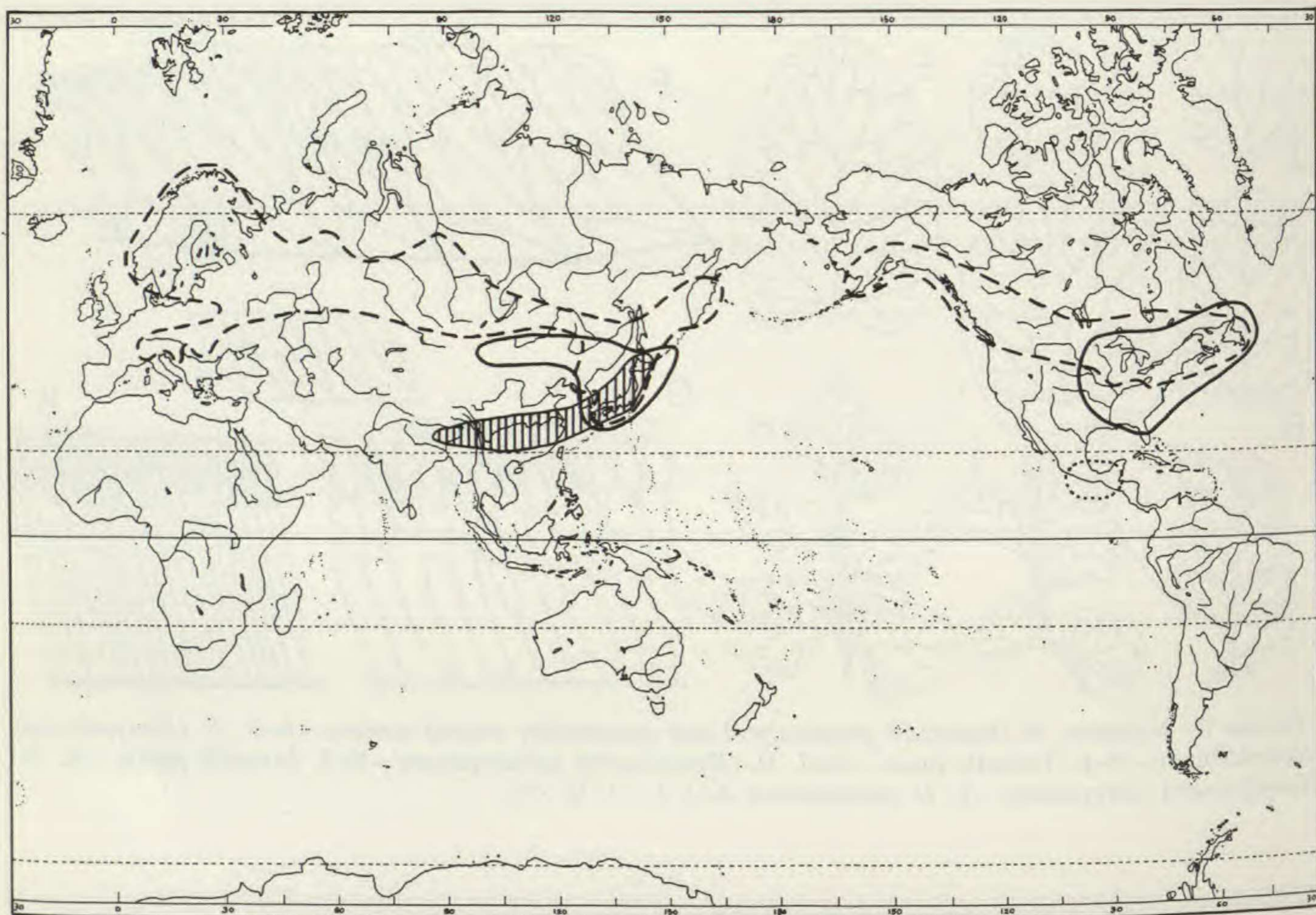
FIGURE 9. Distribution of onocleoid ferns. Solid line, *Onoclea subsibilis*; vertical lines, *O. orientalis*; dotted line, *Matteuccia hintonii*; dashed line, *M. struthiopteris*.

central and southern Europe, and Japan. Most of the fossils are fragments of leaves with reticulate venation, however.

Regarding the taxonomic relationships, Kato and Sahashi (1980) considered that each species of the onocleoid ferns is distinct, *O. sensibilis* and *Matteuccia hintonii* are relatively primitive, and *O. orientalis* and *M. struthiopteris* are derived. Further, that *Onoclea sensibilis* and *Matteuccia hintonii* originated from a common ancestor is suggested by the resemblance in the sagenioid venation of sterile leaves, the compoundly pinnate fertile leaves, and spore ornamentation. From the distribution pattern and presumed taxonomic affinities it is suggested that the onocleoid ferns originated somewhere in Central or North America. *Onoclea orientalis* might have developed in Asia from an *O. sensibilis*-like ancestor whereas *M. struthiopteris* might have originated in North America from a *M. hintonii*-like ancestor and later spread widely in the Northern Hemisphere.

DISCUSSION

From a comparison of the pteridophytes known in the Far East and eastern North America, it is evident that the pteridophyte floras are similar between these two areas, as is the case of the seed plants. It is, however, rather difficult to discuss phytogeographic relationships between any two areas based solely on the present distribution patterns of the extant species. In most cases the distribution of the plants is in good accordance with the geohistory of the areas concerned, and pteridophytes are not exceptional in this respect, despite their easy dispersal by spore. The distribution of pteridophytes is also influenced by environmental factors, especially by such climatic conditions as temperature and moisture, which in turn influence pteridophytes during the entire life cycle from spore germination through sporophyte maturation. Moreover, the distribution of the pteridophytes is strongly dependent upon the vegetation of the areas in which they grow.

The climatic factors influence the vegetation and thus indirectly delimit the distribution. Because the climate in the Far East is more similar to that in eastern North America than to that in western and central North America, at least a part of the geographic similarity of Far East–eastern North American pteridophytes is regulated by such climatic and ecological conditions.

We examined the taxonomic relationships of some apparently identical or vicarious species occurring in temperate North America and Japan, and from these deduced the phytogeographic relationships of each species, although the assumptions are derived from incomplete evidence. The indication is that the apparently identical and vicarious species under consideration have their own phylogenetic background, that the similarity of their present distribution patterns is due to dispersal with allied forests, and that during that time there has been some evolutionary change. Further elucidation of the taxonomic relationships of those species with reference to the morphology, cytology, genetics and ecology surely will contribute to the understanding of the dynamic aspects of the geographic relationships of the fern floras of temperate North America and eastern Asia.

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